Nerita fortidentata, a New Gastropod from the Neogene of Panamá, with Comments on the Fossil Record of *Nerita* in Tropical America

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ABSTRACT

Nerita fortidentata new species is described from the Neogene of Bocas del Toro, Panamá. It is most closely related to the Recent Caribbean *N. fulgurans* Gmelin, 1791. The fossil record and biogeography of tropical American *Nerita* are reviewed. At least two lineages of *Nerita* present in tropical America during the Tertiary have become restricted in the Recent fauna to the Indo-West-Pacific region.

INTRODUCTION

Neritid gastropods are prominent members of tropical rocky intertidal communities. Because the fossilization potential of these animals is poor, little is known about the historical development of the genus *Nerita* Linnaeus, 1758. It was, therefore, of considerable interest to find an excellently preserved specimen of an apparently hitherto unrecognized species from the Neogene of tropical America. Here we describe the new species and review briefly some biogeographically interesting aspects of the history of the genus *Nerita* in tropical America.

METHODS

Species of *Nerita* are distinguished conchologically by characters of shape, apertural dentition, external sculpture, form and sculpture of the parietal callus, and the shape and sculpture of the calcareous operculum. Two ratios are especially helpful in describing the overall shell form of *Nerita* (Vermeij, 1973). The first is globosity, G, defined as the distance H_1 between the dorsal surface of the body whorl and the center of the parietal callus divided by the geometric mean between the shell's major diameter D_1 and minor diameter D_2: $G = H_1/(D_1D_2)^{1/2}$. The second ratio is the degree of basal excavation. The plane of the parietal callus typically lies at an angle to the horizontal when the shell lies aperture-down on a flat surface. The greater the angle, the greater is the degree of basal excavation. An approximation of the degree of basal excavation is given by the ratio $E = H_2/H_1$, where H_2 is the distance from the horizontal plane on which the shell rests to the dorsal surface of the body whorl.

SYSTEMATIC DESCRIPTION

Class **Gastropoda**
Subclass **Prosobranchia**
Order **Neritacea**
Family **Neritidae**

Genus *Nerita* Linnaeus, 1758

Type species: *Nerita peloronta* 1758, Recent, tropical Western Atlantic.

Subgenus *Theliostyla* Mörch, 1852

Type species: *Nerita albicilla* Linnaeus, 1758, Recent, Indo-West-Pacific.

Nerita (*Theliostyla*) *fortidentata* new species
(figures 1, 2)

Diagnosis: Shell thick, moderately globose (G = 0.59), base little excavated (E = 1.10), apex of spire barely raised above rest of shell. Outer lip very thick, inner edge with 12 strong teeth; two teeth nearest spire very large and protruding, as is third tooth from abapical end of lip; columellar lip with two strong centrally placed teeth; adapical portion of parietal region with a fold of about the same size and strength as adapical tooth, which curves into aperture; sculpture consisting of 21 regularly-spaced flat-topped smooth spiral cords, which flare slightly from base to barely overhang incised interspaces about one-third the width of ribs; parietal callus small, its surface sculptured with about 10 strong ridges that bear up to 3 large granules each; holotype shows faint radial color pattern of alternating continuous and discontinuous prosocline bands of off white and grey-black; operculum unknown.

Figure 1. *Nerita fortidentata* new species, from Bocas del Toro, Panamá. Holotype, USNM 423644, height 19.7 mm. Apertural view, showing thickened outer lip and enlarged teeth on adapical portion of outer lip.

Figure 2. *Nerita fortidentata* new species, from Bocas del Toro, Panamá. Holotype, UNSM 423644, height 19.7 mm. Abapertural view.

Holotype: United States National Museum number 423644. Major diameter 21.3 mm, minor diameter 16.9 mm, H_1 11.2 mm, H_2 12.3 mm, standard shell height 19.7 mm (apex abraded), standard shell diameter 19.9 mm, shell thickness at midpoint of outer lip 3.5 mm.

Type locality: Panamá, Province of Bocas del Toro, Archipelago of Bocas del Toro, Punta Robalo quadrangle, Island of Cayo Agua, eastern side about 400 meters south of Punta Nispero on the shoreline in clayey, tuffaceous, quartzose, blue-grey siltstones with dense shelly horizons. We have followed Woodring (1982) in referring to the Late Miocene–Pliocene deposits of the Bocas del Toro area as the Limónes Formation. The true relationships between the Miocene–Pliocene of Bocas del Toro with respect to the Costan Rican Limónes Formation and the Gatun Formation of the Canal Zone have not been elucidated. Laurel Bybell of the U.S.G.S. (personal communication) has assigned a preliminary age of Late Miocene to Early Pliocene to the locality from which the holotype of *N. fortidentata* was collected. This age determination is based on the presence of the calcareous nannofossils *Sphenolithus abies* Deflandre, *in* Deflandre and Fert, 1954 (last occurrence middle Pliocene), and *Discoaster brouweri* Tan, 1927 (first occurrence middle Miocene). Thomas M. Cronin, U.S.G.S. (personal communication), examined the ostracode faunas from several adjacent localities of the same formation on Cayo Agua. He noted a remarkable similarity between the ostracodes from these samples and the ostracode fauna described by van den Bold (1967) from the type Gatun Formation of the Canal Zone. On the basis of these similarities he suggests a preliminary age of Late Miocene for this fauna. Harry Dowsett, also of the U.S.G.S. (personal communication), examined the planktic foraminifera from an adjacent locality of the same formation on Cayo Agua and found an assemblage indicative of planktic zone N17–N18 (Late Miocene–Early Pliocene). The consensus at this stage, therefore, is that the beds from which *N. fortidentata* was collected are Late Miocene to Early Pliocene in age.

Remarks: The new species clearly belongs to the subgenus *Theliostyla* Mörch, 1852 (type *N. albicilla* Linnaeus, 1758), which is characterized by granulate sculpture on the parietal region, a barely protruding spire, and well-developed external spiral sculpture. Among the four Recent species of this subgenus in tropical America, *N. fulgurans* Gmelin, 1791, bears the closest resemblance to *N. fortidentata*. Measurements of 17 specimens of *N. fulgurans* in the Vermeij collection from the Atlantic coasts of Panamá, Costa Rica, Venezuela, and Jamaica show that this species is less globose (G = 0.54 ± 0.020, range 0.50–0.57) and basally much more excavated (E = 1.27 ± 0.05, range 1.21–1.39) than is the new species. *Nerita funiculata* Menke, 1851, the Recent eastern Pacific cognate of *N. fulgurans*, is also less globose (G = 0.51 ± 0.04, range 0.42–0.58, based on 15 specimens in the Vermeij collection from Costa Rica, Panamá, and Ecuador) and more excavated (E = 1.28 ± 0.15, range 1.13–1.60) than is *N. fortidentata*. Both *N. fulgurans* and *N. funiculata* have weaker and more numerous denticles on the outer lip, weaker and more finely granulated ridges on the parietal region, and spiral cords that are more numerous and more variable in size on the body whorl (18–35 in *N. fulgurans*, usually more than 30 in *N. funiculata*). The spiral cords of *N. fulgurans* show a tendency to bifurcate on the body whorl, whereas no such tendency is seen in *N. fortidentata*. The three subspecies of *N. ascensionensis* Gmelin, 1791, from islands in the tropical south Atlantic (Vermeij, 1970) differ from *N. fortidentata* by having a nearly smooth parietal region and by the very weak dentition on the outer lip. The West Indian *N. tessellata* Gmelin, 1791, differs from *N. fortidentata* by having low rounded spiral cords broken irregularly by high and low areas correlating to the characteristic black and white checkered pattern found in this species, a finely granulated parietal region of relatively large extent, and a weakly denticulated outer lip (Russell, 1941).

Jung (1965) recorded *Nerita fulgurans* from the Middle Miocene and Upper Pliocene of Venezuela, but he pointed out that his specimens differed from Recent shells by having stronger apertural dentition and a less concave

(that is, less excavated) parietal region. Later Jung (1969) found a similar shell in the Late Miocene Melajo Clay Member of the Springvale Formation of Trinidad. Like the Venezuelan material, the shell from Trinidad has only 16 ribs, but instead of having 2 centrally placed columellar teeth, as in the Venezuelan material, the Trinidad specimen has one upper tooth which curves into the aperture (this upper tooth is probably equivalent to the parietal fold found on the type of *N. fortidentata*) and 2 somewhat lower denticles. Jung tentatively referred both lots to *N. exuvioides* Trechmann, 1935, a species described on the basis of one incomplete specimen from the Pliocene of Carriacou in the Grenadines. Jung (1971) redescribed this latter specimen as having only 12 ribs whose edges overhang the adjacent interspaces. Vokes (1983) clarified the status of *N. exuvioides* when she described a very strongly ribbed shell with 11 ribs from the Gatun Formation of Panamá. This specimen closely resembles the one from Carriacou and is clearly referable to *N. exuvioides*. We believe that Jung's (1965, 1969) specimens from Venezuela and Trinidad belong neither to *N. fulgurans* nor to *N. exuvioides*, but instead to our new species, *N. fortidentata*. This species appears therefore to be intermediate in sculpture between *N. exuvioides* with only 11–12 ribs and the Recent *N. fulgurans*, usually with more than 21 ribs. The relationship between *N. fortidentata* and the Late Oligocene or Early Miocene *N. tampaensis* Dall, 1892, from the Tampa Formation of Florida is unclear. *Nerita tampaensis*, whose granulated parietal region suggests placement in *Theliostyla*, is a small species with weakly developed apertural dentition and highly variable external sculpture, some shells being nearly smooth whereas others have fine spiral cords of varying sizes.

The shape of *N. fortidentata* suggests that this species inhabited the upper zones of rocky shores. *Nerita fulgurans*, its most similar living relative, is usually found in areas of reduced salinity, such as the mouths of harbors (Russell, 1941) or protected embayments. Vermeij (1973) showed that shells with low globosity, high basal excavation, weak sculpture, and relatively broad apertures with weak dentition are found in middle to lower intertidal species of *Nerita*; whereas species with a globose, little excavated, strongly sculptured shell and a small aperture bordered by strong teeth are found at higher shore levels. The latter shell form is especially characteristic of the subgenera *Cymostyla* von Martens, 1887, and *Ritena* Gray, 1858. Of the living and fossil members of the subgenus *Theliostyla*, most of which live in the middle zones of the intertidal, *N. fortidentata* most closely approaches species of *Ritena*. Other fossils collected with *N. fortidentata*, including *Oliva*, *Olivella*, *Conus*, *Natica*, *Polinices*, *Strombus*, *Phalium*, *Dentalium*, and *Corbula*, suggest a variety of different environments, implying post-mortem transport and mixing of assemblages.

BIOGEOGRAPHY OF AMERICAN *NERITA*

Among the fossil species of *Nerita* that have been described from late Eocene and younger strata in tropical America, at least two have close affinities with living Indo-West-Pacific species. *Nerita listrota* Woodring, 1973, from the late Eocene (?) Gatuncillo Formation of Panamá has a finely ribbed shell with a peripheral keel, fine teeth on the outer lip, 7 teeth on the columellar lip, and a sparsely papillate parietal region. Woodring (1973) noted the striking similarity between *N. listrota* and the recent mangrove-associated *N. planospira* Anton, 1839 (the type and only known species of the subgenus *Ilynerita* von Martens, 1887) from the tropical Indo-Pacific. He doubted that the two species were closely related, in part because *N. planospira* has 5 rather than 7 columellar denticles. We consider the similarities to be so numerous that an inference of close relationship seems warranted. If *N. listrota* belongs to the subgenus *Ilynerita*, as we believe it does, that subgenus may be added to the growing list of taxa whose distributions became restricted to the Indo-West-Pacific during the Tertiary (Vermeij, 1986). As Vokes (1983) points out, *N.* (*Theliostyla*) *exuvioides* may represent a second lineage that has become restricted (as *N. exuvia* Linnaeus, 1758) to the Indo-West-Pacific. *Nerita exuvioides* differs from the Western Pacific *N. exuvia* chiefly by having 11 instead of 14 strong overhanging spiral cords on the body whorl.

The other fossil species of *Nerita* that have been described from late Eocene and younger deposits in tropical America do not easily fit with any living members of the genus. These are *N. hadra* Woodring, 1973, from the late Eocene (?) Gatuncillo Formation of Panamá and *N. oligopleura* Dall and Ochsner, 1928, from the Pleistocene of the Galapagos. *Nerita hadra* has very fine spiral threads on the body whorl and a smooth parietal region, whereas *N. oligopleura* has 3 broad spiral ribs on the body whorl.

Although the record of *Nerita* in tropical America is very meager, the history of the genus points to multiple instances of extinction and geographical restriction. It is too early to assess the scope of these changes, but the record of *Nerita* suggests that intertidal species have been no less affected by events leading to extinction and restriction than have species from the better-sampled fossil environments of subtidal bottoms.

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